BIOMECHANICS OF WATER-PUMPING BY *CHAETOPTERUS VARIOPEDATUS* RENIER: KINETICS AND HYDRODYNAMICS

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Although a number of previous studies have contributed to an understanding of the mechanism by which *Chaetopterus variopedatus* pumps water through its tube (Joyeux-Laffuie, 1890; Enders, 1909; Berrill, 1927; MacGinitie, 1939; Wells, and Dales, 1951; Dales, 1969; Aksyuk and Sveshnikov, 1971; Brown, 1975), the functional design and operation of the integrated three-segment pump system have not been examined in detail. In addition, there has been virtually no systematic attempt to gather data which would permit a quantitative assessment of the pumping performance to be made. This paper presents an operational analysis of the pumping mechanism of *Chaetopterus* which draws on the approaches employed in mechanical and hydraulics engineering.

MATERIALS AND METHODS

Source and maintenance of animals

Specimens of *Chaetopterus* were obtained from Pacific Bio-Marine Laboratories, Inc., Venice, California. Aquarium maintenance procedures and the details of the artificial glass tube-houses are given in earlier papers (Brown, Bdzil and Frisch, 1972; Brown, 1975; Brown and Rosen, 1977).

Mechanical events

In order to correlate the mechanical events of the pumping cycle with the fluctuations in water flow through the tube-house, an apparatus was developed which permitted recording of the top and side views of an actively pumping animal and, simultaneously, the static discharge pressure. The viewing chamber, reservoirs, and photographic set-up have been previously described in detail (Brown, 1975). For pressure measurements, a machined Lucite coupling of the same internal diameter as the glass house was attached to one end of the tube. A static pressure opening, perpendicular to the water flow and 1 cm from the end of the tube, led directly to a Statham UGP-5 low-pressure diaphragm and Universal transducer. Signals from the preamplifier/meter were fed into a Texas Instruments Servo/Riter (0.1 mV full-scale) amplifier/linear recorder. A light bamboo pushrod was attached to the pen of the recorder and positioned so that a paper indicator arrow at the end of the pushrod was within the field of view of the camera. Calibration of the pressure transducer was done before and after each period of filming by lowering the water level in the reservoirs by 1.0 mm and observing the recorder response. Correlation of activity with pressure (and hence flow) changes

was accomplished by comparing data from frame-by-frame analysis of films with the records from the strip-chart recorder.

Flow rate

The rate of water flow through the tube was measured by means of a bubble flow-meter. This design has the combined advantages of generating virtually no back-pressure as well as measuring the velocity of the entire water column, rather than just certain parts. For this purpose, a 15 cm glass tube of internal cross-sectional area slightly greater than that of the terminal tube constriction was interposed between the Lucite coupling and the reservoir. Indicator marks 10 cm apart were scribed on the tube, and the volume of the tube between the marks precisely determined. An air bubble could be injected *via* hypodermic syringe and flexible tubing through an injection port in the coupling. For any single determination, a series of ten bubbles was injected into the discharge current and the elapsed time between the marks determined by electronic stop-watch for each bubble. A mean transit time and, ultimately, an average volume flow rate could then be calculated. Since simultaneous recording of pressure changes also gave the stroke rate, the mean stroke volume could readily be determined.

Oxygen consumption

The concentrations of oxygen in the water at the inflow and discharge ends of the tube were determined by means of a YSI model 57 oxygen meter. Water samples were pumped by means of a Cole Parmer peristaltic pump through a flow chamber (volume = 0.7 ml) past the electrode membrane at a rate of 1.0 ml/min until a stable reading was obtained. Appropriate corrections for atmospheric pressure, salinity, and temperature were made. The oxygen consumption of an actively pumping worm was determined by taking the difference in oxygen concentrations between inlet (mean of two determinations) and discharge ends of the tube and multiplying by the mean volume flow rate. Measurements of oxygen consumption by inactive worms were done according to the procedure of Dales (1969).

Performance measurements

In determining the performance characteristics of an individual worm, the following procedure was followed: (1) acclimatize worm in a glass tube-house for at least 1 week; (2) transfer tube to experimental set-up for at least 12 hrs; (3) measure and record atmospheric pressure and water temperature; (4) determine oxygen concentration of incurrent water supply; (5) calibrate pressure transducer; (6) start pressure/rate recorder; (7) when stroke rate steady, measure volume flow rate; (8) determine oxygen concentration of discharge current; (9) remeasure volume flow rate; (10) remeasure oxygen concentration of incurrent water supply; (11) recalibrate pressure transducer. At this point the pressure/rate recording would be examined to ascertain if constant performance (as judged by stroke rate and pressure output) had been maintained throughout the sampling interval. If within the sampling period the stroke rate varied by more than 2 strokes/min or the peak discharge pressures varied by more than ± 0.2 mm

H_2O, the entire procedure was repeated. If the performance of the worm was consistent within these limits, the procedure was continued as follows: (12) remove worm from tube, blot and determine wet weight; (13) transfer worm to sea water containing 0.075% w./v. tricaine methansulfonate ("MS-222", Sigma); and finally (14) when the worm was immobile, determine O_2 consumption (standard metabolic rate). The total procedure, although laborious, provides direct measurement or permits computation of nearly all relevant performance characteristics for each experimental animal.

Results

The tube-house as a water conducting cylinder

Since the geometry and dimensions of the conduit are of great importance in determining the overall performance characteristics of any liquid pumping system, these parameters will be considered first. The tube-house of *Chaetopterus* is equivalent, in the present context, to a pump piston-chamber plus all of the pipes and "fittings." It is constructed of layers of protein fibers embedded within an acid mucopolysaccharide matrix (Zola, 1967; Brown and McGee-Russell, 1971). This composite material renders the tube pliable but inelastic for all practical purposes. Enders (1906) has given a general description of the methods by which a worm builds and modifies its tube, and two features of the construction process are especially pertinent for the present consideration. First, new layers of protein/polysaccharide are continuously applied to the inner surface of the tube by the worm. This results in the inner surface being always smooth and somewhat slick or slimy (presumably due to the mucopolysaccharide component). Secondly, during its lifetime a worm periodically enlarges its tube to accommodate its increasing bulk. These periodic renovations are carried out upon relatively short segments of the tube at any one time and are influenced by the physical surroundings. Therefore, the shape and size of a tube varies from one worm to another, as well as from one time to another for any individual worm.

In an attempt to determine whether there exist any constant features of tube design, twenty-five recently collected tubes and their living worm occupants were examined and measured. The tubes were selected to include as wide a size range as possible, and to include a variety of shapes—from nearly straight to markedly contorted. The tubes were measured as follows: total length, internal diameter at 1-cm intervals, and minimum internal diameter of the terminal openings. For the worms, wet weight, diameter at segment 12, and total length (extended and contracted) were measured. Such data led to the following conclusions: the length of the tube is poorly correlated with the "size" (any measure) of the worm inhabitant, with the exception that the tubes were always longer than the extended worm; the average internal diameter of main body of the tube was closely correlated with the "size" (especially diameter) of the worm, and hence is considered to be the best measure of the "size" of the tube; even in the most contorted tubes, the variation in internal diameter of the main part of the tube was small—being less than $\pm 10\%$ of the mean internal diameter; and the terminal openings of the tubes were invariably constricted—the mean ratio of orifice cross-sectional area to mean tube cross-sectional area was 0.190 ± 0.080 (s.d.).
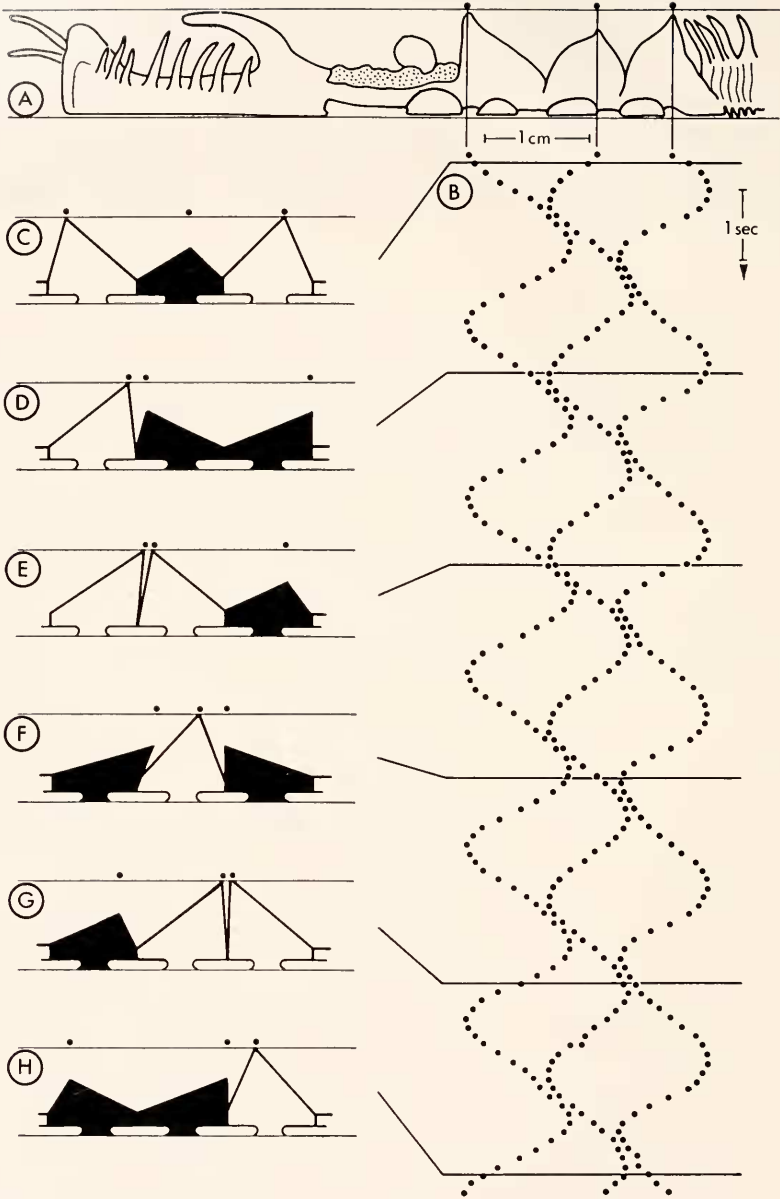
FIGURE 1. A, Orientation and posture of *Chaetopterus* during water-pumping (measurements taken at reference points indicated); B, frame-by-frame analysis of displacements of piston segments during six consecutive strokes; C-H, diagrammatic representation of position and shape of piston segments at the times indicated (white = power phase; black = recovery phase).

Qualitative performance

The moving parts of a commercial reciprocating pump consist, at a minimum, of power train, pistons, and valves (Hicks, 1957). The analogous elements are represented in segments 14–16 of *Chaetopterus* by the intrinsic musculature (largely the promotor and remotor muscles), the posterior segmental wall, and the parapodial margins, respectively (Brown, 1975). Figure 1, A-H, illustrates the basic working features of the integrated 3-piston pump mechanism of *Chaetopterus*. Noteworthy are the virtually identical repetition of the motions (axial displacements illustrated) which occur during the six successive stroke cycles presented here, as well as the high degree of precision in the coordination of the pumping and valve movements, both within each individual segment and between the three adjacent segments (see also, Brown, 1975, Fig. 8). It is evident that during normal pumping the waves of activity are retrograde; that is, they begin anteriorly at segment 14 and move posteriorly to segment 16. The phase difference between piston units would be predicted to be $1/3$, and this is found to be the case observationally. The smooth transitions observed between segment 16 (most posterior) and segment 14 (most anterior) argue for a high degree of intersegmental coordination during continuous pumping activities, and this is also suggested by the work of Berrill (1927). Comparison of simultaneous recordings of the piston movements with fluid discharge pressure (Fig. 2) gives a clearer picture of the detailed operation of the moving elements of the system. It can be seen that the discharge pressure (and hence water flow) is pulsatile, with output maxima corresponding to the periods of maximum sustained rearward velocity of the piston segments, and output minima occurring during the overlap and changeover between the different piston/valve units. As before, the coordination of events during the changeover between segments 16 to 14 is indistinguishable from those of the structurally-adjacent segments (*i.e.*, 14 to 15 and 15 to 16). The data clearly show that at least one piston is in its power phase at all times, and also that at least one set of valves is in its closed configuration at all times. These latter two features have great functional significance, since they ensure that fluid flow is continuously maintained throughout periods of active pumping.

With regard to the direction of flow, it is my experience that a worm does not reverse the direction of the effective piston stroke during normal water pumping activities. Rather, a worm turns end-for-end in its tube in order to reverse the direction of flow in the system. Thus, although the functional inlet and discharge ends of the pump system are reversed, the water flow across the worm remains directed anterior to posterior. This constancy of anterior-to-posterior water flow is clearly dictated by the linearly polarized structures associated with the unique mucous-bag feeding mechanism of the animal (MacGinitie, 1939). That worms may, exceptionally, reverse the direction of beating has been previously reported by Enders (1909) and Werner (1959), but it is likely that such reversals were associated with tube-cleaning activities, which are produced by a motor sequence quite different from that normally employed (Brown and Rosen, 1977). As stated earlier (Brown, 1975), *Chaetopterus* shows no evidence of preferring one end of its tube over the other insofar as direction of water flow is concerned. In contrast, there are clear preferences in body orientation (ventral side down) and position (closer to the incurrent opening). These latter
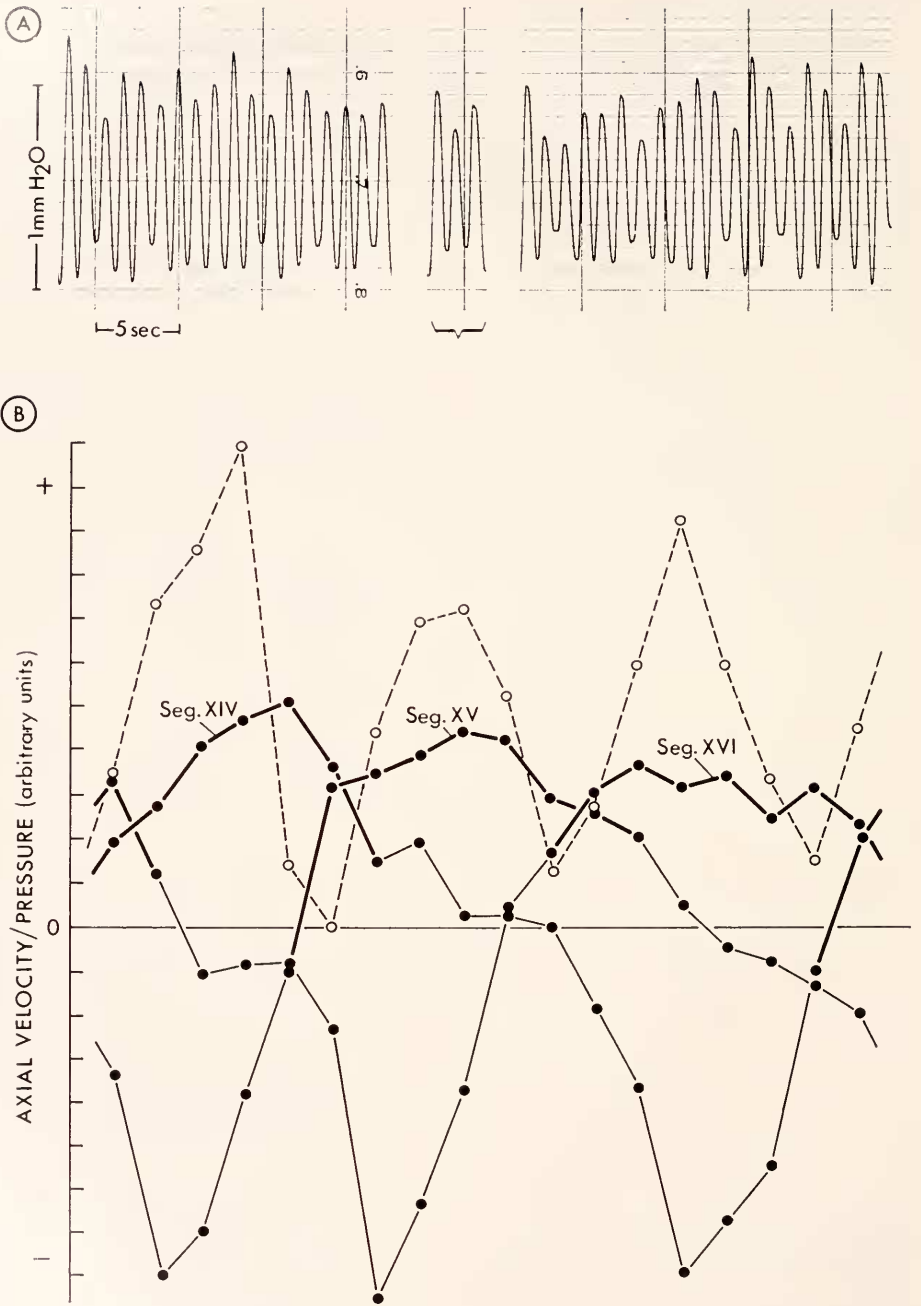
FIGURE 2. A, Strip-chart recording of static discharge pressure during water-pumping;
and B, frame-by-frame analysis of the one complete stroke cycle indicated (dashed line shows

characteristics, however, appear not to be critical factors in the coordinated operation of the pump mechanism.

Quantitative performance

It is readily observable that an individual animal has considerable latitude in the rate of pumping which it can accomplish. In addition, the extensibility of the three pump segments permits a worm to achieve variable displacement during the power stroke. These two capabilities clearly enable worms to make volume-flow adjustments by changing either stroke rate or stroke volume, or by a combination of the two. The particular circumstances under which a worm would choose one method over another are quite unknown. In fact, even the relationship between pumping rate and such obvious external conditions as temperature, dissolved oxygen or carbon dioxide, and/or the presence of nutrients has not been examined systematically. The previously published data on the quantitative aspects of water-pumping by *Chaetopterus,* along with results from the present experiments, are summarized in Table I. With the exception of the flow rate estimate of Aksyuk and Sveshnikov (1971), the data appear reasonably consistent, given the small number of animals which have been measured and the many unknown factors which may influence performance. The measured and calculated values of Wells and Dales (1951), Dales (1969) and the present paper are at least of the same order of magnitude.

DISCUSSION

Notwithstanding the conventional description of *Chaetopterus* tube-houses as being "U-shaped", it is evident that such tubes may be constructed in a variety of forms. Such differences in overall shape undoubtedly reflect the environmental peculiarities of the site where each tube-house was constructed (Enders, 1906; 1909). However, since all of the houses examined were obviously functional, it appears unlikely that the gross shape of the tube is of critical importance in the water-pumping mechanism. In contrast, certain other features of tube-house design can be shown to bear directly on the water conducting function. For example, the tubes of *Chaetopterus* are unique among those of the Chaetopteridae in possessing identical terminal openings of relatively large cross-sectional area (for descriptions of the tubes of *Spiochaetopterus, Telepsavus, Phyllochaetopterus, Ranzanides,* and *Mesochaetopterus,* see Barnes, 1964; 1965). Such apertures are an obvious requirement if any large volume of water is to be transported through the tube. The nonpolarity of the tubes, together with the ability of worms to reverse themselves rapidly, permit either end of a tube-house to serve as a functional intake or discharge opening. This is of considerable importance in maintaining unobstructed water flow during potentially-fouling water conditions (Brown and Rosen, 1977). The terminal constrictions serve several functions. Besides acting to keep larger predators out of the tube, such constrictions serve to increase

position of pushrod indicator (pressure) ; solid lines are derived axial velocities of the three piston segments; positive velocity values for power stroke, negative values for recovery stroke; heavy lines indicate lateral margins of segments pressed against inner wall of tube).

TABLE I

Quantitative performance of Chaetopterus *during water-pumping activity; values in brackets were calculated from data given in the reference cited.*

Parameter (units)	MacGinitie, 1939	Wells and Dales, 1951	Dales, 1969	Aksyuk and Sveshnikov, 1971	This paper, mean (range)
Number of animals	2	—	1	—	5
Wet weight (grams)	—	—	4.32	—	4.52 (3.18–6.40)
Water temperature (°C)	—	11–16	15	24	16
Stroke rate (strokes/sec)	1.07, 1.03	—	—	[0.21–0.97]	0.53 (0.45–0.67)
Stroke volume (cm³/stroke)	—	0.27	—	[5.2]	1.01 (0.88–1.17)
Flow rate (cm³/sec)	—	0.27	0.13	*ca.* 5.0	0.54 (0.43–0.70)
O₂ consumption [cm³/g·hr)]	—	—	0.225	—	0.124 (0.050–0.200)
R.Q.	—	—	1.0	—	—
Discharge pressure (N/m²)	—	—	[10–20]	—	10–20

the water velocity at the incurrent and discharge openings above that in the main part of the tube. In the present sample of tubes the orifice velocity is about five and one-half times greater, but it is apparently more than twenty-five times greater in the large *Chaetopterus* tubes from the Sea of Japan measured by Aksyuk and Sveshnikov (1971). Although high intake velocity may be important in facilitating capture of actively swimming zoo-plankton, as suggested by Aksyuk and Sveshnikov (1971), a high discharge velocity is probably equally important in serving to eject feces and other potentially-fouling particles to a considerable distance from the tube (*cf.*, analogous situations in sponges, acsidians, etc.). In addition, it is likely that such high water velocities serve to prevent sessile organisms from settling on the orifice rims and subsequently obstructing a free flow of water.

The relative invariance in the internal diameter of a tube-house reflects the manner in which it is constructed—*i.e.*, as layers secreted from the convex "ventral shield" located on the anterior 12 segments of the worm (Brown, unpublished observations). This secretory "shield" also acts as a template upon which the protein/polysaccharide layers assume their final (curved) shape. The isodiametric nature of the major portion of the tube is functionally significant in that it permits a worm to pump water from virtually any location within its tube with equal (and presumably optimal) effectiveness. In addition, the slick/slimy nature of the newly-secreted wall of the tube acts, in concert with epithelial mucins secreted from segments 14–16, as a lubricant to minimize friction between the moving piston segments and the wall of the tube.

In operation, *Chaetopterus* is most closely analogous to a reciprocating positive-displacement pump (Wilson, 1950; Brown, 1975). The pumping system of *Chaetopterus* can be further categorized as being "compound" (since more than one piston/valve unit is involved) and "single-acting" (since liquid is pumped only during half of the stroke cycle) (Hicks, 1957). In a simple single-acting power reciprocating pump, the discharge curve (showing output pressure or

flow) invariably takes the form of rectified sine wave, with flow pulses (lasting for one-half the complete stroke cycle) alternating regularly with periods of zero flow. The addition of other single-acting piston/valve units with overlapping power strokes has the dual advantages of reducing the magnitude of pulsations as well as assuring that flow will be continuous. The multiple piston/valve units of *Chaetopterus,* although differing from commercial pumps by being arranged in series rather than in parallel, achieve precisely the same effects—namely, dampened pulsations and continuous flow. In *Chaetopterus,* pulse dampening is undoubtedly augmented by the deformability of the "pistons", as well as the smooth integration of motions during periods of transition from one pump segment to another (Fig. 2B). It is of special interest to note that in compound single-acting power reciprocating pumps the *minimum* number of piston/valve units which can yield a continuous flow is three (Hicks, 1957). The fact that *Chaetopterus* possesses just this number of pump segments may indicate the existence of a strong selective advantage in being able to maintain a continuous water flow during periods of active pumping. It may be further mentioned that *Chaetopterus* compares very favorably with the better mechanical pumps (Hicks, 1957; Wilson, 1950) in having the ability, during "operation", to vary the stroke rate, vary the stroke volume, and reverse the direction of flow. Its self-cleaning (Brown and Rosen, 1977) and self-repair (Enders, 1906) capabilities are "features" unrivalled in mechanical systems.

From the present data, quantitative estimates of power output, power input, and aerobic mechanical efficiency can be made. Power output is obtained from the volume flow rate multiplied by the total pressure drop across the "pump" (see Alexander, 1975, pp. 28–30, for a well-illustrated discussion). In the case where the mucous feeding bag is not deployed (the situation which prevailed during all of the present experiments), the discharge pressure varied in a pulsatile fashion between 1–2 mm H_2O ($= 10$–20 N/m^2). Although the pressure on the intake side of the piston segments was not measured simultaneously, it may be assumed to be of equal magnitude. Taking 15 N/m^2 to be a reasonable average value for both the intake and the discharge pressures, the sum total pressure drop across the pump segments is on the order of 30 N/m^2. Taking 0.5 cm^3/sec as the mean flow rate, the power ouput is calculated to be 1.5×10^{-5} Joules/sec. At the same time, the total oxygen consumption due to pumping activity, per worm, was measured to be *ca.* 0.5 cm/hr^3. Employing Dales' (1969) measured R.Q. of 1.0 (and therefore an equivalent of 5.09 calories of energy liberated per cm^3 of O_2 consumed), the equivalent aerobic power input is calculated to be 3×10^{-3} Joules/sec. The overall water-pumping efficiency of a nonfeeding *Chaetopterus* is thus seen to be about 0.5%. In the alternative case, *i.e.,* during periods when the mucous bag is stretched across the lumen of the tube, it is possible that the power output is somewhat greater than the above estimate would suggest. For this to be true, the pressure differential across the mucous sheet would have to exceed 3 mm of H_2O, with no diminution in flow rate. Although it is theoretically possible to determine this value directly (*i.e.,* by measuring the pressure at a point between the mucous sheet and the first pump segment), numerous attempts to do so have thus far proved unsuccessful. Moreover, indirect calculation of the total porosity of the mucous sheet is not feasible at present, in spite of the availability of data

on the effective size of the individual pores (MacGinitie, 1945; but see Jørgensen, 1966, for a critical discussion). However, inasmuch as there are no discernable differences in the pumping behavior of worms with, or without, a mucous sheet present (indicative, for example, of different "loads" on the pump mechanism), and the area of the mucous bag is nearly $8 \times$ greater than the cross-sectional area of the tube (calculated from MacGinitie, 1939), it is tentatively concluded that the power developed by a worm, while feeding, is not likely to be significantly different from the value reported here.

As a final point, an assessment of the nature of the "work" performed by the pump mechanism of *Chaetopterus* may be attempted. Reference to analyses of comparable mechanical pumping systems (Hicks, 1957; Wilson, 1950) provides an approach to the problem. The total work performed by most reciprocating liquid pumps is the sum of three identifiable components: first, the work done to lift a mass of fluid to a higher level in the gravitational field; secondly, the work done to overcome resistance to flow (= friction) caused by the inner surface of the piping and various "fittings" (elbows, valves, constrictors, etc.); and thirdly, the work done (at each power stroke) to accelerate a mass of fluid to a greater velocity (= inertial resistance). In determining the magnitude of the lift component, reference must be made to the height differential between the liquid surfaces at the supply and delivery ends of the pump. For *Chaetopterus,* it is evident that this difference is zero, since the level(s) of the ocean's surface above the intake and discharge ends of the pumping segments are effectively identical at any given instant. *Chaetopterus,* therefore, does no lifting work, and thus corresponds to the so-called "transfer pumps" used widely in industry to move liquids horizontally from one container to another. Given a liquid pumping system in which the work done is limited to that overcoming frictional and inertial resistances, procedures developed in the field of haemodynamics for the analysis of pulsatile flow in rigid-walled ducts (Lightfoot, 1974, pp. 104–113) may be employed. Computation of α^2 (a characteristic frequency-dependent Reynolds' number) from the formula $\alpha^2 = R^2 \omega/v$ (where R = internal radius of tube; ω = stroke frequency, and v = kinematic viscosity) leads to the conclusion that 95% of the work accomplished by *Chaetopterus* during pumping is devoted to overcoming intertial resistance.

The only comparable performance estimates of water-pumping by a worm are those of Chapman (1968) for the echiuroid, *Urechis caupo.* In this animal (which propels water through its burrow by means of peristaltic contractions of the body wall) the calculated power output was in the range of $0.65–3.27 \times 10^{-5}$ Joules/sec, with an aerobic mechanical efficiency of approximately 1.4%. These values are remarkably similar to those reported here for *Chaetopterus.* It would be of considerable interest to have quantitative data on the performance of other animal "pumps", particularly of different mechanical design, to compare with those of *Urechis* and *Chaetopterus.*

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Summary

1. The activities of the three water-pumping segments of *Chaetopterus variopedatus* are correlated in detail with the fluctuations in water flow through the tube-house.

2. The qualitative performance and design features of the worm's pumping mechanism are compared to those of mechanical reciprocating pumps.

3. Quantitative data on volume flow rate, stroke rate, discharge pressure, and oxygen consumption yield estimates of power output (1.5×10^{-5} Joules/sec) and aerobic efficiency (0.5%).

4. In its natural habitat, *Chaetopterus* does no lifting work, but rather functions solely as a transfer pump.

5. Calculations show that, of the work accomplished by *Chaetopterus* during pumping, 95% is devoted to overcoming inertial resistance.

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